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Correlates of reproductive success in a population of nine-banded armadillos

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Abstract: We used microsatellite DNA markers to identify the putative parents of 69 litters of nine-banded armadillos (*Dasypus novemcinctus*) over 4 years. Male and female parents did not differ in any measure of body size in comparisons with nonparents. However, males observed paired with a female were significantly larger than unpaired males, although paired females were the same size as unpaired females. Females categorized as possibly lactating were significantly larger than females that were either definitely lactating or definitely not lactating. There was no evidence of assortative mating: body-size measurements of mothers were not significantly correlated with those of fathers. Nine-banded armadillos give birth to litters of genetically identical quadruplets. Mothers (but not fathers) of female litters were significantly larger than mothers of male litters, and maternal (but not paternal) body size was positively correlated with the number of surviving young within years, but not cumulatively. There were no differences in dates of birth between male and female litters, nor were there any significant relationships between birth date and maternal body size. Body size of either parent was not correlated with the body sizes of their offspring. Cumulative and yearly reproductive success did not differ between reproductively successful males and females. Average reproductive success (which included apparently unsuccessful individuals) also did not differ between males and females. The majority of adults in the population apparently failed to produce any surviving offspring, and even those that did usually did so in only 1 of the 4 years. This low reproductive success is unexpected, given the rapid and successful range extension of this species throughout the southeastern United States in this century.

Résumé : Nous avons utilisé des marqueurs d'ADN microsatellites pour identifier les parents putatifs de 69 portées de Tatous à neuf bandes (*Dasypus novemcinctus*) au cours d'une période de 4 ans. Les parents mâles et femelles ne différaient par aucune mesure de leur corps des individus non parents. Par ailleurs, les mâles pairés à une femelle étaient significativement plus gros que les mâles non pairés, alors que les femelles pairées ou non pairées étaient de la même taille. Les femelles classifiées comme possiblement nourricières étaient plus grosses que les femelles certainement nourricières ou les femelles certainement non nourricières. Aucun indice ne nous a permis de conclure à l'existence d'accouplements discriminatoires : les mesures corporelles des mères n'étaient pas significativement reliées à celles des pères. Le Tatou à neuf bandes donne naissance à des portées de quadruplés génétiquement identiques. Les mères (pas les pères) des portées de femelles se sont avérées significativement plus grosses que les mères des portées de mâles et la taille des mères (pas celles des pères) était en corrélation positive avec le nombre de jeunes survivants chaque année, mais pas cumulativement. Les portées de mâles et de femelles n'avaient pas des dates de naissance significativement différentes et il n'y avait pas de corrélation significative entre la date de naissance et la taille de la mère. La taille de l'un ou l'autre parent n'était pas en corrélation avec la taille de la progéniture. Le succès de la reproduction, annuel ou cumulatif, ne différait pas chez les mâles et les femelles qui avaient eu une reproduction réussie. Le succès moyen à la reproduction (calculé en tenant compte aussi des individus qui n'ont pas réussi) ne différait pas chez les mâles et les femelles. La majorité des adultes de la population n'ont apparemment pas produit de jeunes qui ont survécu et ceux qui l'ont fait ont généralement eu des petits seulement 1 année sur les 4. Ce taux de reproduction faible est étonnant étant donné l'expansion rapide et l'établissement de l'espèce dans tout le sud-est des États-Unis au cours de ce siècle.

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Introduction

One of the goals of evolutionary biologists is to identify the features of individuals that translate into differential reproductive success (Clutton-Brock 1988). For example, in many species, individuals that produce offspring are larger than nonparental individuals, either because increased size promotes the winning of contests over access to mates (e.g., Howard 1988; Le Boeuf and Reiter 1988) or because individuals have more energy to invest in the production of offspring (Trivers 1972; Gittleman and Thompson 1988; Clutton-Brock 1991). Body size may not only influence an

individual's ability to reproduce, but also may influence features of the offspring subsequently produced. For example, larger parents may produce larger offspring, thus increasing juvenile survivorship (Clutton-Brock et al. 1988; Hoogland 1995), or they may bias the sex ratio of their young to produce the more costly sex (Trivers and Willard 1973; Clutton-Brock and Iason 1986).

Nine-banded armadillos (*Dasypus novemcinctus*) are relatively asocial, nocturnal, burrowing mammals (Newman 1913; Kalmbach 1943; Taber 1945; Talmage and Buchanan 1954; Galbreath 1982; McBee and Baker 1982). Breeding usually occurs during the summer, with delayed implantation of the blastocyst occurring in autumn (Hamlett 1932; Enders 1966; Storrs et al. 1988; McDonough 1992). Young are born in litters of genetically identical quadruplets the following spring (Newman and Patterson 1910; Patterson 1913; Hamlett 1932; Enders 1966; Storrs and Williams 1968; Prodöhl et al. 1996) and first emerge from their natal burrows in May or early June. Obtaining data on reproductive success for this species is difficult for several reasons. First, because the animals are normally solitary, active at night, and found in thickly vegetated habitats, observations of mating are rare. However, McDonough (1992, 1997) was able to describe "pairing behaviour" in which an adult male and adult female maintained proximity to one another during the breeding season (see also Jacobs 1979). Females were typically observed paired with only a single male, but males were often observed paired with two or three different females (McDonough 1992). These data suggest that *D. novemcinctus* is polygynous, but confirming such assertions requires data showing that pairing associations lead to successful matings (Prodöhl et al. 1998). Second, juveniles are active earlier in the day than are adults (McDonough and Loughry 1997*a*). Thus, there are few observations of juveniles interacting with adults that could be used to infer parentage. Finally, home-range overlap between a set of juveniles and an adult cannot be used to assign maternity or paternity because home ranges of juveniles typically overlap those of several adults (Breece and Dusi 1985; McDonough 1992). Genetic screening appears to be the only feasible way to obtain reliable estimates of maternity and paternity (and, consequently, reproductive success) in this species.

In a previous study, we used microsatellite DNA markers to identify the putative parents of 69 litters of nine-banded armadillos produced from 1992 to 1995 at a site in Florida (Prodöhl et al. 1998). While not completely unambiguous, these data provide the best current estimate of paternity and maternity for individuals in the population. In this paper, we use these assignments to evaluate potential differences between parents and nonparents and to examine whether attributes of either parent are associated with attributes of the subsequently produced young.

Methods

Data collection

We studied nine-banded armadillos on the Tall Timbers Research Station near Tallahassee, Leon County, Florida, during the summers (June–August) of 1992–1995 (McDonough and Loughry 1997*a*; Loughry and McDonough 1998). Armadillos were captured using a large dip net attached to a 1- to 1.5-m pole, sexed, and weighed, and five body-size measurements (all in centimetres) were obtained: (1) tail base: the circumference of the tail at its juncture with the body near the pelvic shield of the carapace; (2) tail length: the length of the tail from the base to the tip (animals in whom a portion of the tail was missing were not measured); (3) front carapace: the length of the anterior edge of the scapular shield of the carapace (i.e., at the juncture with the head); (4) front band: the length of the posterior edge of the scapular shield; and (5) back band: the length of the anterior edge of the pelvic shield, i.e., the ninth, most posterior, movable band. In addition, females were classified as lactating if the nipples were large, protruding, and swollen at the base, definitely not lactating if the nipples were barely visible, and possibly lactating if nipple size was intermediate between the first two categories (Loughry and McDonough 1996). Animals were marked for permanent identification using ear tags and, beginning in 1993, passive injectable transponder (PIT) tags. Finally, a small tissue sample for genetic studies was taken from one or both ears using an ear-notcher.

Parentage assignment

We captured juveniles from 69 litters over the 4 years of the study. Genetic assignment of maternity and paternity to these litters is described in Prodöhl et al. (1998). Briefly, seven polymorphic loci were identified in the population using microsatellite DNA markers (Prodöhl et al. 1996). Maximum-likelihood procedures (Thompson 1976, 1986; Meagher and Thompson 1986, 1987; Thompson and Meagher 1987) were used to identify parents of particular litters. Three levels of analysis were used. LOD scores (the likelihood ratio between parent–offspring status and unrelatedness) were calculated for individuals of each sex separately and then as parental-pair combinations (see Table 3 in Prodöhl et al. 1998). Finally, spatial data were used to identify the individual with the highest LOD score that was also in closest proximity to a given litter. This individual was designated as one of the parents of that litter. In some cases, genetic data could not resolve paternity or maternity conclusively. For example, a female might have been identified as the most likely mother of more than one litter in a year. In these cases we classified the adult as the parent of the litter to which it was closer and assigned the next most likely individual as the parent of the other litter. Because males may be polygynous (McDonough 1992), we did not do this in cases where the same male was identified as the most likely father of more than one litter in the same year. With these criteria we were able to identify at least one parent for 68 of the 69 litters. In 67 of these 68 cases we were able to identify a putative father (n = 46 different males) and in 61 we were able to identify the mother (n = 46 different females).

An individual's reproductive success was defined as the number of juveniles that we were able to capture from each litter produced by that individual. In cases where we did not capture or observe all four juveniles from a litter, we assumed that the missing young had died. While it is possible that these juveniles were present and we just never saw them, two lines of evidence support our assumption. First, litters were captured in the summer, when genetic and behavioral data both indicate spatial clustering of littermates (Loughry and McDonough 1994, 1998; Prodöhl et al. 1996; Loughry et al. 1998). Litters do not usually break up until the fall, so it would be unusual to observe a litter of which only some members were present while the additional members were elsewhere. Second, juvenile mortality, particularly from predation, can be high (McDonough and Loughry 1997*b*). Given the timing of our captures, mortality seems a more likely explanation for missing juveniles than dispersal. Nonetheless, in addition to analyzing reproductive success in terms of the number of juveniles that we actually caught, because litter size is essentially fixed at four, we performed a second set of analyses in which an individual's "maximum reproductive

Table 1. Average body sizes of adult male and female armadillos that produced female and male litters or produced no offspring.

	Fathers		Mothers		Nonparents	
	Female litters	Male litters	Female litters	Male litters	Females	Males
Body mass (kg)	4.16 (0.09)	4.23 (0.07)	4.29 (0.08)	4.02 (0.09)	4.11 (0.06)	4.07 (0.05)
Front carapace (cm)	21.59 (0.17)	21.63 (0.14)	22.16 (0.16)	21.46 (0.22)	21.63 (0.12)	21.54 (0.10)
Front band (cm)	34.17 (0.31)	34.38 (0.21)	36.39 (0.24)	34.74 (0.30)	35.13 (0.18)	34.01 (0.14)
Back band (cm)	36.16 (0.37)	36.16 (0.25)	38.30 (0.28)	36.63 (0.30)	37.22 (0.21)	35.58 (0.16)
Tail base (cm)	15.34 (0.15)	15.48 (0.12)	15.99 (0.12)	15.56 (0.14)	15.62 (0.10)	15.29 (0.08)
Tail length (cm)	33.02 (0.36)	33.03 (0.54)	33.52 (0.38)	32.78 (0.37)	32.62 (0.26)	33.42 (0.23)
n	32–35	23–30	18–28	19–27	70–78	93–114

Note: Values in parentheses are standard errors. Sample sizes vary because some animals were lacking some measurements.

success" was determined by assigning a value of 4 to every litter produced by that individual.

Analyses

We compared masses and body sizes of adults that produced male litters with those that produced female litters and with nonparents of the same sex. Measurements of the same individual in different years were treated as independent because of the possibility of changes in size over time. Although our body-size measures are correlated with one another (Loughry and McDonough 1996), multiple comparisons were employed because not all individuals had all measurements and because we wanted to provide a more complete picture of the extent of differences in size between individuals. As a result, however, we used a family-wide p value of 0.01 (Bonferroni correction; Rice 1989) in all statistical comparisons using the five body-size measurements. Statistically significant differences in body mass were recognized at $p = 0.05$.

The possibility of assortative mating was examined by performing regressions between the body-size measurements of fathers and mothers for each litter. We further examined body-size effects on reproduction by comparing the body sizes of females that were classified as lactating, possibly lactating, or nonlactating and by comparing body sizes of individuals that were observed paired with a member of the opposite sex during the breeding season with those of individuals that were never observed paired.

Yearly and cumulative reproductive success was compared between males and females by means of t tests. These analyses were performed using data from just successful individuals as well as including all individuals. For analyses of yearly reproductive success, litters were included for which the mother could not be identified. This was done because females only give birth to one litter a year (Enders 1966), so each litter represents the reproductive success of a different female. The proportions of males and females that were classified as reproductive and nonreproductive over the entire study were compared using a χ^2 test. Armadillos are relatively long-lived (one captive female is currently 23 years old; S. McPhee, personal communication), so the estimates of cumulative reproductive success that we present should not be confused with lifetime reproductive success.

Associations between parental attributes and attributes of subsequently produced offspring were analyzed in two ways. First, regressions were used to examine whether parental body size was correlated in any way with the number of surviving offspring. This analysis was performed for the number of young surviving per year and also for the cumulative number of young produced over all 4 years by all reproductively successful individuals. For the latter analysis, we also used our estimate of maximum reproductive success (this could not be done for the within-year analysis because, since a value of four offspring was assigned to all litters, there was no variation in litter size within a given year). Second, regressions were used to determine if body-size measurements of parents were correlated with those of offspring. In this analysis we used the average of the measurements of all juveniles in a litter. There is a potential problem with this analysis in that juveniles were caught at different points during the summer. Juvenile body size was strongly correlated with calendar date (all measures, $p < 0.001$, df = 1,65; calendar date begins with 1 June as day 0). Thus, a multiple regression was used in which the two independent variables were parental body size and calendar date and the dependent variable was juvenile body size.

Finally, for mothers, the timing of reproduction was analyzed with regressions between the date of birth of a litter and maternal body size. Birth date was determined using the method of Jacobs (1979) (also see McDonough et al. 1998) by measuring the body mass of a juvenile at first capture (masses were averaged for all juveniles in a litter), assuming a linear mass gain of 10.6 g/day, and back-dating to a mass of 100 g (which is the typical birth mass; McDonough et al. 1998). Differences in birth dates between male and female litters were then compared using a t test.

Results

Parental attributes

Body sizes of genetically identified male parents did not differ significantly from those of apparently unsuccessful males or between fathers of male litters and fathers of female litters (ANOVAs, all $p > 0.11$) (Table 1). However, there were significant differences between females in length of the front (ANOVA, $F = 9.86$, $p = 0.0001$) and back bands ($F = 6.84$, $p = 0.002$) (Table 1). While not significant using the Bonferroni correction, there was a trend for length of the front carapace to differ among females as well ($F = 3.78$, $p = 0.026$). Post hoc pairwise comparisons using Scheffé tests showed that mothers of female litters had significantly longer front carapaces than mothers of male litters ($p < 0.05$) and significantly longer front and back bands than both mothers of male litters and apparently nonreproductive females (all $p < 0.05$).

There were no significant correlations between the body size of the mother of a litter and the father of that litter (all $p > 0.06$, $n = 29$–54 for each body-size measure), suggesting that no size-based assortative mating occurred.

Males observed paired with a female during the breeding season were significantly larger than unpaired males (Table 2), but there were no size differences between paired and unpaired females (Table 2). Females classified as possibly lactating were larger than females classified as either definitely lactating or definitely not lactating (Table 3). However, lactating females did not differ in size from nonlactating females (Table 3).

Table 2. Average body sizes of adult male and female armadillos observed paired with a member of the opposite sex during the breeding season and of adults not observed paired.

	Males		Females	
	Paired	Unpaired	Paired	Unpaired
Body mass (kg)	4.38 (0.07)	4.07 (0.05)*	4.19 (0.07)	4.11 (0.05)
Front carapace (cm)	22.06 (0.20)	21.48 (0.09)*	21.56 (0.23)	21.71 (0.10)
Front band (cm)	34.93 (0.20)	34.00 (0.13)**	35.27 (0.33)	35.28 (0.16)
Back band (cm)	36.47 (0.26)	35.65 (0.15)	36.82 (0.36)	37.39 (0.18)
Tail base (cm)	15.77 (0.18)	15.26 (0.07)*	15.89 (0.15)	15.63 (0.08)
Tail length (cm)	33.59 (0.69)	33.19 (0.20)	32.83 (0.61)	32.75 (0.23)
n	18	135	22	98

Note: Values in parentheses are standard errors. Within-sex comparisons (*t* tests): *, $p = 0.02$; **, $p = 0.01$.

Table 3. Average body sizes of adult female armadillos that differed in lactational status.

	Lactating	Possibly lactating	Nonlactating	*p*	Comparisons
Body mass (kg)	4.17 (0.05)	4.36 (0.09)	4.09 (0.08)	0.07	None
Front carapace (cm)	21.75 (0.15)	22.18 (0.22)	21.64 (0.16)	0.16	a
Front band (cm)	35.27 (0.21)	36.36 (0.33)	35.05 (0.23)	0.006	a, b
Back band (cm)	37.21 (0.22)	38.44 (0.40)	37.17 (0.26)	0.01	a, b
Tail base (cm)	15.70 (0.10)	15.99 (0.17)	15.69 (0.13)	0.28	None
Tail length (cm)	32.35 (0.33)	33.41 (0.62)	32.82 (0.40)	0.26	None
n	49	19	37		

Note: Values in parentheses are standard errors. *p* values are from ANOVAs with df = 2,102; comparisons indicate significant pairwise comparisons from post hoc Scheffé's tests: "a" is possibly lactating versus lactating and "b" is possibly lactating versus nonlactating (there were no significant pairwise comparisons between lactating and nonlactating females).

Associations with juvenile attributes

There were no significant relationships between the date of birth of a litter and any measure of maternal body size for all litters combined (all $p > 0.30$; for samples sizes see Table 4) or when male and female litters were examined separately (male litters, all $p > 0.66$, $n = 19$–27; female litters, all $p > 0.42$, $n = 18$–28). In addition, there was no significant difference in the birth dates of male versus female litters (males, 77.19 ± 9.32 days, $n = 31$; females, 68.42 ± 6.35 days, $n = 38$; $t = 0.80$, $p = 0.43$; days are numbered beginning with 1 January as day 0).

Maternal and paternal body sizes were not significantly correlated with the average size of a juvenile in the resulting litter (based on partial *F* ratios derived from a multiple regression with calendar date as the second independent variable; for mothers, all $p > 0.16$; for fathers, all $p > 0.32$). The same was true when relationships between parental body size and body sizes of male and female juveniles were examined separately (for mothers and male litters, all $p > 0.60$, female litters, all $p > 0.17$; for fathers and male litters, all $p > 0.65$, female litters, all $p > 0.08$).

Yearly reproductive success

There were no significant correlations between paternal body size and the number of surviving juveniles produced within a year (Table 4). However, larger maternal body mass was associated with an increased number of surviving young (Table 4). This relationship could have been generated by the difference in body size between mothers of male and female litters, if the number of surviving young was higher in female litters. This did not seem to be the case because the sizes of male and female litters did not differ (males, 1.32 ± 0.12, $n = 31$; females, 1.61 ± 0.18, $n = 38$; $t = 1.28$, $p = 0.21$).

Table 4. Correlations between paternal and maternal body sizes and the number of juveniles still alive per litter.

	Males			Females		
	n	*r*	*p*	*n*	*r*	*p*
Body mass	64	–0.07	0.58	55	0.29	0.032
Front carapace	61	0.02	0.87	54	0.25	0.068
Front band	64	0.05	0.68	54	0.28	0.041
Back band	64	–0.05	0.70	54	0.25	0.064
Tail base	65	0.09	0.49	55	0.24	0.080
Tail length	55	–0.02	0.88	37	0.10	0.550

There were no significant differences in the number of surviving juveniles produced by reproductively successful males and females either when data from all years were pooled (males, 1.67 ± 0.14, $n = 61$; females, 1.48 ± 0.11, $n = 69$; $t = 1.11$, $p = 0.27$) or when each year was examined separately (*t* tests, all $p > 0.13$). Inclusion of reproductively unsuccessful individuals of each sex still produced no difference in reproductive success between males and females when data from all years were pooled (males, 0.59 ± 0.08, $n = 174$; females, 0.69 ± 0.08, $n = 147$; $t = 0.96$, $p = 0.34$) and when each year was examined separately (*t* tests, all $p > 0.32$). A second set of analyses, using maximum reproductive success rather than the number of surviving juveniles, yielded essentially the same results. In 3 of the 4 years of the study (1992, 1993, and 1994) we found no evidence of polygyny (i.e., each litter was produced by a different pair

of adults). Consequently, the reproductive success of reproductively active males and females in each of these years was exactly equal. However, in 1995, six males were identified as the putative fathers of more than one litter (four males were the most likely father of two separate litters and two males apparently sired three separate litters). Because of this, maximum reproductive success was significantly higher for reproductively successful males than for females in this year (males, 5.14 ± 0.45, n = 28; females, 4.0 ± 0.0, n = 36; t = 2.86, p = 0.006) and also when data from all years were pooled (males, 4.52 ± 0.22, n = 61; females, 4.0 ± 0.0, n = 69; t = 2.55, p = 0.012). However, inclusion of reproductively unsuccessful individuals eliminated this difference, both for 1995 (males, 2.06 ± 0.35, n = 70; females, 2.62 ± 0.26, n = 55; t = 1.22, p = 0.22) and when all years were combined (males, 1.59 ± 0.18, n = 174; females, 1.88 ± 0.17, n = 147; t = 1.17, p = 0.24).

Cumulative reproductive success

Unlike with yearly reproductive success, there were no significant correlations between cumulative reproductive success and any measure of maternal or paternal body size. This was true whether we calculated reproductive success in terms of the number of juveniles actually caught (for fathers, all $p > 0.27$, n = 27–40; for mothers, all $p > 0.14$, n = 36–44) or the maximum number of juveniles that could have been produced (for fathers, all $p > 0.19$; for mothers, all $p > 0.13$). In addition, mothers and fathers did not differ in the total number of surviving offspring produced over the 4-year study period (males, 2.11 ± 0.22; females, 2.02 ± 0.22 offspring; n = 46 for each sex; t = 0.28, p = 0.78). The sexes had similar proportions of individuals that were apparently unsuccessful and left no offspring (92 of 138 males and 79 of 125 females; χ^2 = 0.21, p = 0.61). Consequently, there was no significant difference in cumulative reproductive success between males and females when unsuccessful adults were included in the analysis (males, 0.70 ± 0.11 offspring, n = 138; females, 0.75 ± 0.12 offspring, n = 125; t = 0.28, p = 0.78). Using estimates of maximum reproductive success, we still found no differences between males and females in their cumulative reproductive success, either when examining just reproductively successful animals (males, 5.83 ± 0.39; females, 5.30 ± 0.39; t = 1.26, p = 0.21) or when including apparently unsuccessful individuals (males, 1.94 ± 0.27; females, 1.97 ± 0.28; t = 0.07, p = 0.95).

Discussion

This study represents the first attempt to analyze reproductive success in nine-banded armadillos. Our results lead us to conclude that for males, differential reproductive success is not based on any of the attributes of males that were measured, nor do any of these paternal attributes appear to be associated with features of the resulting offspring. On the other hand, larger females were more likely to produce a female litter and to have more juveniles from that litter survive their first summer above ground. Male and female reproductive success was low, but roughly equal. This was true whether one examined reproductive success within years or cumulatively and when only reproductively successful individuals were compared or when all members of the population were included. It is important to remember that these conclusions are preliminary. Our analyses are only as reliable as our assignments of maternity and paternity, which in turn depend on the amount of genetic variation present and the completeness of our sampling effort. Nine-banded armadillos at Tall Timbers are only moderately polymorphic genetically, so ambiguities do arise in assigning parentage using genetic markers only (Prodöhl et al. 1998). In addition, it is likely that some adults and some litters were not captured, so we cannot say conclusively that an individual did not reproduce. However, given the biology of this species, it is unlikely that complete samples can ever be obtained for an entire population. So, while our data are not ideal, they represent an important first step in understanding reproductive success in *D. novemcinctus*.

Differences in body size were associated with differences in mating opportunities for both males and females. Males observed paired with a female were larger than males that were never observed paired. Pairing may represent a form of mate guarding by males (McDonough 1992, 1997), and larger males may be better able to defend females (McDonough 1994). While pairing may indicate a male's ability to obtain access to a female, it is apparently unreliable as a predictor of paternity (Prodöhl et al. 1998). This is further supported by the lack of body-size differences between fathers and nonfathers in the present study, which suggests that although larger males pair more frequently, small males are not excluded from reproduction. While reproductive success appears to be random with respect to male body size, we cannot exclude the possibility that there are other features of males that significantly impact fitness (e.g., home-range size and degree of overlap with reproductive females; Stockley et al. 1996).

Mothers of female litters were larger than mothers of male litters and also larger than reproductively unsuccessful females. Given these results, according to sex-ratio theory, juvenile females should be more costly to produce (Trivers and Willard 1973; Clutton-Brock and Iason 1986). Why this should be so in nine-banded armadillos is not obvious. Recruitment of juveniles into the local population is low for both sexes (Loughry and McDonough 1998), so it seems unlikely that daughters are more expensive because of competition with the mother over resources (Silk 1983). However, the number of surviving offspring was positively correlated with maternal body size within years, so if larger females produce larger daughters, then large females might be expected to produce primarily female litters to maximize their reproductive success. Unfortunately, this hypothesis seems unlikely because we could find no correlation between maternal and juvenile body sizes. Further explanation of the relationships between maternal body size, litter sex ratio, and reproductive success will require detailed data on juvenile dispersal and maternal investment in offspring. Currently, there are virtually no data on these subjects.

Female body size also varied with lactational status, females classified as possibly lactating being larger than females that were definitely lactating or definitely not lactating. It is not obvious why this is so. One explanation might be that the possibly lactating category is composed of females that have finished nursing. Lactation is energetically expensive (Oftedal 1984; Thompson 1992), so females that

have finished nursing may be able to start accumulating energy reserves. This could make these females larger than females that are currently lactating and thus suffering a large energetic cost. However, this would not explain why possibly lactating females were also larger than females that were definitely not lactating.

Observations of adults paired during the breeding season showed that males were often observed with more than one female, but females were usually observed paired with only one male (McDonough 1992). These data suggested that nine-banded armadillos might be polygynous, an assertion that is supported by reports of sexual dimorphism (body size of males greater than that of females; see McBee and Baker 1982; McDonough 1992). Our data on reproductive success indicate otherwise. Polygynous species typically exhibit a pattern in which a few males monopolize most matings (Emlen and Oring 1977; Clutton-Brock 1989; Arnold and Duvall 1994). These successful males typically have much higher reproductive success than reproductively successful females in the same population. In addition, because most females mate, while many males are excluded from reproduction, the proportion of reproductively unsuccessful individuals is much higher for males than for females (Emlen and Oring 1977; Clutton-Brock 1989; Arnold and Duvall 1994). Contrary to these expectations, in this study we found that reproductively successful males produced as many offspring as did reproductively successful females (their ranges were also similar: 1–7 for males and 1–8 for females), and the proportions of males and females that were reproductively unsuccessful were equivalent. However, our data do provide some evidence of polygyny. As mentioned earlier, six males were identified as the most likely father of more than one litter in 1995. Thus, it appears that while polygyny may occur in our population, it is rare enough that it does not dramatically influence the average reproductive success of males. It is also important to note that McDonough's (1992, 1997) data on pairing were collected at a study site in Texas. Social organization, including mating systems, can vary between populations (Lott 1991), so the relative absence of polygyny at Tall Timbers need not imply that it is unimportant in other parts of the species' range.

There are two striking features of our data that are somewhat paradoxical. First, reproductive success was low for reproductively successful males and females. Second, a large proportion of adults were apparently unsuccessful at producing any offspring over the 4 years of our study. *Dasypus novemcinctus* has colonized much of the southern United States during this century (Humphrey 1974; Taulman and Robbins 1996), suggesting a relatively high reproductive output. It is difficult to see how such a rapid range extension could be generated by the low reproductive success that we found at Tall Timbers. However, it is important to remember that these are long-lived animals and that our estimates of reproductive success may not accurately reflect the lifetime output of an individual. Assuming that reproductive success is actually low, it may be that reproductive output varies with recency of colonization. Tall Timbers was colonized by armadillos in the early 1970s (Stevenson and Crawford 1974). It may be that at that time, reproductive success was higher, but declined as the habitat became relatively saturated with individuals. Data from populations at the very edge of the species' distribution will be needed to test this hypothesis.

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References

Arnold, S.J., and Duvall, D. 1994. Animal mating systems: a synthesis based on selection theory. Am. Nat. **143**: 317–348.

Breece, G.A., and Dusi, J.L. 1985. Food habits and home ranges of the common long-nosed armadillo *Dasypus novemcinctus* in Alabama. *In* The evolution and ecology of armadillos, sloths, and vermilinguas. *Edited by* G.G. Montgomery. Smithsonian Institution Press, Washington, D.C. pp. 419–427.

Clutton-Brock, T.H. (*Editor*). 1988. Reproductive success. University of Chicago Press, Chicago.

Clutton-Brock, T.H. 1989. Mammalian mating systems. Proc. R. Soc. Lond. Ser. B Biol. Sci. **236**: 339–372.

Clutton-Brock, T.H. 1991. The evolution of parental care. Princeton University Press, Princeton, N.J.

Clutton-Brock, T.H., and Iason, G.R. 1986. Sex ratio variation in mammals. Q. Rev. Biol. **61**: 339–374.

Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1988. Reproductive success in red deer. *In* Reproductive success. *Edited by* T.H. Clutton-Brock. University of Chicago Press, Chicago. pp. 325–343.

Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection and the evolution of mating systems. Science (Washington, D.C.), **197**: 215–223.

Enders, A.C. 1966. The reproductive cycle of the nine-banded armadillo (*Dasypus novemcinctus*). *In* Comparative biology of reproduction in mammals. *Edited by* I.W. Rowlands. Academic Press, New York. pp. 295–310.

Galbreath, G.J. 1982. Armadillo. *In* Wild mammals of North America. *Edited by* J.A. Chapman and G.A. Feldhamer. Johns Hopkins University Press, Baltimore, Md. pp. 71–79.

Gittleman, J.L., and Thompson, S.D. 1988. Energy allocation in mammalian reproduction. Am. Zool. **28**: 863–875.

Hamlett, G.W.D. 1932. The reproductive cycle of the armadillo. Z. Wiss. Zool. **141**: 143–157.

Hoogland, J.L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago.

Howard, R.D. 1988. Reproductive success in two species of anurans. *In* Reproductive success. *Edited by* T.H. Clutton-Brock. University of Chicago Press, Chicago. pp. 99–113.

Humphrey, S.R. 1974. Zoogeography of the nine-banded armadillo in the United States. BioScience, **24**: 457–462.

Jacobs, J. 1979. Behavior and space usage patterns of the nine-banded armadillo (*Dasypus novemcinctus*) in southwestern Mississippi. M.S. thesis, Cornell University, Ithaca, N.Y.

Kalmbach, E.R. 1943. The armadillo: its relation to agriculture and game. Texas Game, Fish and Oyster Commission, Austin.

Le Boeuf, B.J., and Reiter, J. 1988. Lifetime reproductive success in northern elephant seals. *In* Reproductive success. *Edited by*

T.H. Clutton-Brock. University of Chicago Press, Chicago. pp. 344–362.

Lott, D.F. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge.

Loughry, W.J., and McDonough, C.M. 1994. Scent discrimination by infant nine-banded armadillos. J. Mammal. **75**: 1033–1039.

Loughry, W.J., and McDonough, C.M. 1996. Are road-kills valid indicators of armadillo population structure? Am. Midl. Nat. **135**: 53–59.

Loughry, W.J., and McDonough, C.M. 1998. Spatial patterns in a population of nine-banded armadillos. Am. Midl. Nat. **140**: 161–169.

Loughry, W.J., Dwyer, G.M., and McDonough, C.M. 1998. Behavioral interactions between juvenile nine-banded armadillos (*Dasypus novemcinctus*) in staged encounters. Am. Midl. Nat. **139**: 125–132.

McBee, K., and Baker, R.J. 1982. *Dasypus novemcinctus*. Mamm. Species, **162**: 1–9.

McDonough, C.M. 1992. The behavior and ecology of nine-banded armadillos (*Dasypus novemcinctus*) in south Texas. Ph.D. thesis, University of California, Davis.

McDonough, C.M. 1994. Determinants of aggression in nine-banded armadillos. J. Mammal. **75**: 189–198.

McDonough, C.M. 1997. Pairing behavior of the nine-banded armadillo (*Dasypus novemcinctus*). Am. Midl. Nat. **138**: 290–298.

McDonough, C.M., and Loughry, W.J. 1997*a*. Influences on activity patterns in a population of nine-banded armadillos. J. Mammal. **78**: 932–941.

McDonough, C.M., and Loughry, W.J. 1997*b*. Patterns of mortality in a population of nine-banded armadillos, *Dasypus novemcinctus*. Am. Midl. Nat. **138**: 299–305.

McDonough, C.M., McPhee, S.A., and Loughry, W.J. 1998. Growth rates of juvenile nine-banded armadillos. Southwest. Nat. **43**: 462–468.

Meagher, T.R., and Thompson, E.A. 1986. The relationship between single parent and parent pair genetic likelihoods in genealogy reconstruction. Theor. Popul. Biol. **29**: 87–106.

Meagher, T.R., and Thompson, E.A. 1987. Analysis of parentage for naturally established seedlings of *Chamaelirium luteum* (Liliaceae). Ecology, **68**: 803–812.

Newman, H.H. 1913. The natural history of the nine-banded armadillo of Texas. Am. Nat. **47**: 513–539.

Newman, H.H., and Patterson, J.T. 1910. The development of the nine-banded armadillo from primitive streak to birth, with special reference to the question of polyembryony. J. Morphol. **21**: 359–423.

Oftedal, O.T. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. Symp. Zool. Soc. Lond. No. 51. pp. 33–85.

Patterson, J.T. 1913. Polyembryonic development in *Tatusia novemcinctus*. J. Morphol. **24**: 559–684.

Prodöhl, P.A., Loughry, W.J., McDonough, C.M., Nelson, W.S., and Avise, J.C. 1996. Molecular documentation of polyembryony and the micro-spatial dispersion of clonal sibships in the nine-banded armadillo, *Dasypus novemcinctus*. Proc. R. Soc. Lond. Ser. B Biol. Sci. **263**: 1643–1649.

Prodöhl, P.A., Loughry, W.J., McDonough, C.M., Nelson, W.S., Thompson, E.A., and Avise, J.C. 1998. Genetic maternity and paternity in a local population of armadillos assessed by microsatellite DNA markers and field data. Am. Nat. **151**: 7–19.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**: 223–225.

Silk, J.B. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive activities. Am. Nat. **121**: 56–66.

Stevenson, H.M., and Crawford, R.L. 1974. Spread of the armadillo into the Tallahassee–Thomasville area. Fla. Field Nat. **2**: 8–10.

Stockley, P., Searle, J.B., Macdonald, D.W., and Jones, C.S. 1996. Correlates of reproductive success within alternative mating tactics of the common shrew. Behav. Ecol. **7**: 334–340.

Storrs, E.E., and Williams, R.J. 1968. A study of monozygotic quadruplet armadillos in relation to mammalian inheritance. Proc. Natl. Acad. Sci. U.S.A. **60**: 910–914.

Storrs, E.E., Burchfield, H.P., and Rees, R.J.W. 1988. Superdelayed parturition in armadillos: a new mammalian survival strategy. Lepr. Rev. **59**: 11–15.

Taber, F.W. 1945. Contribution on the life history and ecology of the nine-banded armadillo. J. Mammal. **26**: 211–226.

Talmage, R.V., and Buchanan, G.D. 1954. The armadillo (*Dasypus novemcinctus*): a review of its natural history, ecology, anatomy and reproductive physiology. Rice Inst. Pam. Monogr. Biol. No. 4.

Taulman, J.F., and Robbins, L.W. 1996. Recent range expansion and distributional limits of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. J. Biogeogr. **23**: 635–648.

Thompson, E.A. 1976. Inference of genealogical structure. Soc. Sci. Inf. **15**: 477–526.

Thompson, E.A. 1986. Pedigree analysis in human genetics. Johns Hopkins University Press, Baltimore, Md.

Thompson, E.A., and Meagher, T.R. 1987. Parental and sib likelihoods in genealogy reconstruction. Biometrics, **43**: 585–600.

Thompson, S.D. 1992. Gestation and lactation in small mammals: basal metabolic rate and the limits of energy use. *In* Mammalian energetics: interdisciplinary views of metabolism and reproduction. *Edited by* T.E. Tomasi and T.H. Horton. Cornell University Press, Ithaca, N.Y. pp. 213–259.

Trivers, R.L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man. *Edited by* B. Campbell. Aldine Press, Chicago. pp. 136–179.

Trivers, R.L., and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science (Washington, D.C.), **179**: 90–92.